Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees

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Abstract: Much of the debate about reciprocity in humans and other primates hinges on proximate mechanisms, or more precisely, the contingency of one service on another. While there is good evidence for long-term statistical contingencies of services given and received in primates, results for short-term behavioral contingencies are mixed. Indeed, as we show here controlled experiments using artificial tasks and explicit turn-taking were unlikely to find short-term effects. We therefore used more naturalistic experiments to test for short-term contingencies of grooming on food sharing and vice versa in one group of chimpanzees and two groups of bonobos. Overall, we found significant effects of grooming on food sharing and vice versa, however, in the chimpanzees these effects disappeared when controlling for long-term characteristics of the dyad including services exchanged over the whole study period. In the bonobos, short-term contingencies remained significant which was likely a consequence of considerable tension surrounding monopolizable food resulting in higher rates of grooming and other affiliative behaviors around sharing sessions. These results are consistent with the fact that previous evidence for short-term contingency often involved grooming and that long-term contingency is more commonly observed in primates. We propose that long-term contingency is proximately regulated by a 'relationship score' computed through a tally of past interactions which tend to outweigh recent single events. We therefore suggest that future research into the proximate mechanisms of reciprocity should trace the development of such a score by focusing on newly formed dyads with no history of interactions.

DOI: https://doi.org/10.1016/j.evolhumbehav.2012.09.005

Originally published at:
Jaeggi, A V; De Groot, E; Stevens, J M G; van Schaik, C P (2013). Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. Evolution and Human Behavior, 34(2):69-77.
DOI: https://doi.org/10.1016/j.evolhumbehav.2012.09.005

*Title Page

Mechanisms of reciprocity in primates: Testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees

Running head: Contingent reciprocity in bonobos and chimpanzees

ADRIAN V. JAEGGI[1,2], EVELIEN DE GROOT[3], JEROEN M.G. STEVENS[3], & CAREL P. VAN SCHAIK[4]

[1]Department of Anthropology, University of California Santa Barbara

[2]Sage Center for the Study of Mind, University of California Santa Barbara

[3]Centre for Research and Conservation, Royal Zoological Society of Antwerp, Belgium

[4]Anthropological Institute & Museum, University of Zurich, Switzerland

Correspondence:

Adrian V. Jaeggi, PhD

Department of Anthropology

University of California

Santa Barbara CA 93106

Email: ajaeggi@anth.ucsb.edu

Word count: 9,106

Abstract

Much of the debate about reciprocity in humans and other primates hinges on proximate mechanisms, or more precisely, the contingency of one service on another. While there is good evidence for long-term statistical contingencies of services given and received in primates, results for short-term behavioral contingencies are very mixed. Indeed, controlled experiments using artificial tasks and explicit turn-taking were unlikely to find short-term effects, as we show here. We therefore used more naturalistic experiments to test for short-term contingencies of grooming on food sharing and vice versa in one group of chimpanzees and two groups of bonobos. Overall, we found significant effects of grooming on food sharing and vice versa, however, in the chimpanzees these effects disappeared when controlling for long-term characteristics of the dyad including services exchanged over the whole study period. In the bonobos, short-term contingencies remained significant which was likely a consequence of considerable tension surrounding monopolizable food resulting in higher rates of grooming and other affiliative behaviors around sharing sessions. These results are consistent with the fact that previous evidence for short-term contingency often involved grooming and that long-term contingency is more commonly observed in primates. We propose that long-term contingency is proximately regulated by a 'relationship score' computed through a tally of past interactions which tend to outweigh recent single events. We therefore suggest that future research into the proximate mechanisms of reciprocity should trace the development of such a score by focusing on newly formed dyads with no history of interactions.

Introduction

Reciprocal altruism has received a lot of attention as one of the main evolutionary pathways to stable cooperation among unrelated individuals, both in humans and other primates (Trivers, 1971; Trivers, 2006). Indeed, Trivers (1971) suggested that primates should be predisposed to reciprocal altruism due to their relatively long lifespans, stable group compositions, and individual recognition, allowing for ample future opportunities to reciprocate; and he went on to discuss human friendships as a proximate mechanism for such long-term exchange in our own species. Reciprocal altruism has since received support from theoretical models (reviewed by Nowak 2006) as well as from empirical studies on human foragers (Allen-Arave et al., 2008; Gurven, 2004a, 2004b; Gurven, 2006; Koster, 2011; Patton, 2005; Ziker & Schnegg, 2005) and non-human primates (reviewed by Silk 2002; Schino 2007; Schino and Aureli 2009; Schino and Aureli 2010; Jaeggi and van Schaik 2011). These studies commonly measure services given and received over a long time period and then test for a statistical association between them. Since most such tests were statistically significant (Gurven, 2004a; Jaeggi & van Schaik, 2011) there is good evidence for a *long-term statistical contingency* in many primate species.

Nonetheless, such correlational evidence for reciprocal altruism has been questioned, mainly on the basis of a lack of evidence for a *short-term behavioral contingency* between services given and received (Clutton-Brock, 2009; Hammerstein, 2003). The standard theoretical implementation of reciprocity as an iterated prisoner's dilemma in isolated dyads (e.g. Axelrod and Hamilton 1981) leads to the expectation that every service given is contingent on a

47 previously received service in order to avoid defection. In humans, the expectation of giving
48 upon receiving is explicitly mentioned in some ethnographies on food sharing in small-scale
49 societies (although others emphasize a lack of such expectations; Gurven 2004a), and children
50 seem to develop the faculties for such short-term contingencies around mid childhood (House et
51 al., in review) which coincides with the shift from exclusive household provisioning to
52 communal resources (Haig, 2010). The evidence for such short-term contingency of one service
53 on another in studies on nonhuman primates is however very mixed (see Table 1), and more
54 parsimonious explanations such as mutualism have therefore been endorsed (Clutton-Brock,
55 2009). Understanding this discrepancy between short-term and long-term contingency, and more
56 generally, understanding how reciprocity is regulated on a proximate level, is therefore
57 paramount for drawing inferences about the evolutionary significance of reciprocal altruism for
58 understanding primate and human cooperation.
59
60 (insert Table 1 about here)
61
62 Brosnan and de Waal (2002) were the first to propose possible proximate mechanisms for
63 reciprocity in animals. They suggested three mechanisms with increasing cognitive demands:
64 *Symmetry-based reciprocity*, which is mediated by general characteristics of the dyad such as age
65 or rank differences, kinship or affiliation and does not require any score-keeping; *attitudinal*
66 *reciprocity*, which is mediated by a mirroring of fluctuating attitudes in social partners reflected
67 in changes in recently shown behavior; and *calculated reciprocity*, which is based on mental
68 score-keeping and memory of recent interactions. In practice, symmetry-based reciprocity has
69 often been operationalized as long-term contingency and calculated reciprocity as short-term

70 contingency, with attitudinal reciprocity being either ignored or lumped with one or the other
71 (Brosnan et al., 2009; Dufouret al., 2009; Koyama et al., 2006; Schino & Aureli, 2010; de Waal,
72 1997). Therefore, the proposed evidence for calculated reciprocity largely equates to the effects
73 of one service on another as compiled in Table 1. Most relevant here is a classic study of de
74 Waal (1997) on chimpanzees in which he found that grooming significantly increased an
75 individual's subsequent chances of obtaining food, and that this effect was (i) specific to the
76 groomer, (ii) independent of the current state of the relationship, (iii) behaviorally mediated by
77 decreased resistance to food requests, and (iv) stronger in dyads that rarely groomed. In addition,
78 there was a weak trend for sharing to be followed by more grooming.
79
80 A striking pattern about the tests of short-term contingencies compiled in Table 1 is the
81 strong discrepancy between experimental studies employing a *naturalistic design* (defined here
82 as using naturally occurring behaviors such as grooming, coalitionary support or food sharing in
83 a whole group setting), and those employing a more *artificial design* (experimental tasks such as
84 pulling a tray to deliver food or exchanging tokens, subject pairs isolated from group, alternating
85 roles as donor and recipient). In fact, positive evidence for short-term contingency is
86 significantly associated with a naturalistic design (Fisher's exact $P<0.05$). The same is true when
87 the sample is restricted to studies on great apes. This casts doubt on calculated reciprocity as an
88 underlying mechanism of short-term contingencies, as such a strategy might be expected more in
89 the explicit turn-taking situations of controlled experiments, at least in cognitively advanced
90 species such as great apes (Brosnan et al., 2009; Dufour et al., 2009; Melis et al., 2008;
91 Yamamoto & Tanaka, 2009). At the very least, this suggests that artificial turn-taking
92 experiments fail to trigger the evolved psychology (if present) for calculated reciprocity which

93 would not be surprising given that the subjects' behavior is likely due to behavioral decision
94 rules triggered by certain aspects of the experiment rather than a complete understanding of the
95 task the way the experimenters intended (Jaeggi et al., 2010b, Cronin in press).
96
97 The absence of calculated reciprocity and its operationalizaton as short-term contingency
98 has recently also been highlighted by Schino and Aureli (2009; 2010). They argue that reciprocal
99 exchange should be modeled as a biological market, where commodities are exchanged
100 following the rules of supply and demand in a system driven by *partner choice* (Noë &
101 Hammerstein, 1995; Noë & Hammerstein, 1994). Thus, individuals should preferentially interact
102 with those partners who have provided them with the most benefits in the past, and, imbalances
103 due to differing bargaining power notwithstanding, exchanges are therefore expected to balance
104 out over longer time periods (Schino & Aureli, 2009; 2010).
105
106 Indeed, several studies have shown that exchanges become more balanced with time
107 (Frank & Silk, 2009; Gomes et al., 2009; Schino et al., 2007; Schino & Pellegrini, 2009; Tiddi et
108 al., 2011), which together with the limited evidence for immediate effects of one service on
109 another (Table 1) indicates that primate reciprocity is little affected by recent single events.
110 Furthermore, a clever study by Schino and Pellegrini (2011) shows that even when recent events
111 do increase the chance of immediate reciprocation, individuals do not strategically take
112 advantage of this, suggesting a lack of understanding for short-term contingencies. Schino and
113 Aureli (2009; 2010) therefore urged to take the correlational evidence for long-term contingency
114 seriously and abandon the narrow focus on short-term contingency as the only evidence for true
115 contingency. They propose a mediating role of social bonds or 'friendships' (Silk 2002) as a

116 form of loose emotional book-keeping as a proximate mechanism for the partner choice model,
117 which does not suffer from the constraints of cognitively more demanding models (Schino &
118 Aureli, 2009; 2010). According to the partner choice model, short-term contingencies are
119 therefore only expected in rarely interacting partners where recent events may weigh more
120 heavily.
121
122 Here we attempt to resolve some of this on-going debate by testing for short-term
123 contingencies of grooming on food sharing and vice versa in one group of captive chimpanzees
124 and two groups of captive bonobos. While we test for long-term contingencies elsewhere (Jaeggi
125 et al., 2010; de Groot, 2011), this study provides a valuable test of the models discussed above
126 for various reasons: First, both chimpanzees and bonobos are cognitively advanced species and
127 are therefore expected to be capable of calculated reciprocity. Second, we employ a naturalistic
128 study design which should increase the chances of finding positive evidence for short-term
129 contingencies (Table 1). Third, testing two different species and multiple groups allows us to
130 relate potential differences in short-term or long-term contingencies to social or ecological
131 characteristics while also allowing us to pool data from all subjects in order to maximize
132 statistical power.
133
134 *Hypotheses*
135
136 Following the introduction above, we test the following hypotheses regarding short-term
137 contingencies in our study groups:

- *Short-term contingency*: We test for short-term contingency by looking at the immediate effect of grooming on subsequent food sharing and vice versa. We call this the '*tit-for-tat model*' (see Methods). Under the Brosnan and de Waal (2002) model, some evidence of short-term contingencies is expected in this study as both species should be cognitively capable of calculated reciprocity. Under the partner choice model on the other hand (Schino & Aureli, 2009; 2010), short-term contingencies are expected to be negligible if services given are explained by long-term aspects of the relationship (see below). This should be particularly true for the chimpanzees as long-term contingency of food, grooming and support has been demonstrated previously (Jaeggi et al., 2010a). Therefore, we expand the tit-for-tat model with a number of controls to exclude other explanations:
    - *Partner-specificity*: Short-term contingency has to be partner specific in order to reflect calculated reciprocity. Following de Waal (1997) we test this by adding the effect of grooming by third parties on subsequent food sharing which, if positive, would simply reflect a 'good mood' induced by grooming rather than calculated reciprocity.
    - *Current state of relationship*: Increased food sharing should not simply reflect the state of the relationship between owner and approacher (de Waal, 1997). We control for this by adding the effect of grooming by the owner on subsequent sharing. By itself, such an effect would simply indicate the direction in which services usually flow within the dyad; in interaction with grooming by the approacher it might reflect attitudinal reciprocity.
    - *Social distance*: The contingent effect of grooming on food sharing was found to be more pronounced in socially distant partners (de Waal 1997) which is compatible

with the partner-choice model in which recent events only weigh heavily in dyads who rarely interact (Schino & Aureli, 2009; 2010). We test this by adding an interaction with long-term relationship quality, as a measure of social distance, to the short-term contingency effect.

    - *Long-term contingency*: The partner-choice model would predict that any short-term effects are outweighed by the longer history of the relationship. We test this by adding relationship quality as an independent predictor of food sharing or grooming.
    - *General relationship characteristics*: We control for general effects of kinship, dominance rank, and sex combination by including the appropriate variables as independent predictors. In combination with relationship quality, positive effects of these variables might reflect symmetry-based reciprocity (Brosnan & de Waal 2002).

- *Behavioral mediation*: A contingent effect of grooming on sharing has been suggested to be behaviorally mediated by food owners' decreased resistance to food requests (de Waal, 1997). We test this by analyzing the effects of all aforementioned predictors on the likelihood of food requests being met by a negative or even aggressive reaction. Furthermore, it has also been reported that grooming and other affiliative behaviors are generally increased during feeding sessions in order to reduce the tension surrounding monopolizable food, especially in bonobos (de Waal, 1992). As such increased grooming due to the need to reduce tension could mediate short-term contingency, we also recorded the occurrence of grooming and affiliative contact during feeding sessions, including during approaches to food owners.

Methods

Study groups and observation methods

We studied one group of chimpanzees and two groups of bonobos. Table 2 gives a brief overview of the group compositions and observation periods. In each group there were three dyads comprised of maternal relatives (mother-son, mother-daughter, or maternal half-siblings). Even though paternal relatedness was known through pedigree or genetic paternity analyses, it was not included here as preliminary analyses did not reveal any differences between paternal kin and nonkin. Only one individual was a member of both bonobo groups, which is why we treated them as independent social units. More detailed information on all the subjects and food interaction patterns can also be found elsewhere (Jaeggi et al., 2010a; de Groot, 2011).

(insert Table 2 about here)

To induce food sharing we used monopolizable paper bags filled with fruits and vegetables, as previously reported (Jaeggi et al., 2010a; de Groot, 2011). In most experiments, one or two bags were introduced at a time, either by hiding them in the enclosure or by tossing them to certain individuals in order to balance ownership. Sharing experiments were usually conducted once a day in the chimpanzee group (early afternoon) and twice a day in the bonobo groups (morning, early afternoon) with the exact timing depending on the schedule of regular feedings on that day in the zoos. The apes quickly associated the presence of certain observers with the bag experiments and were generally well aware of any feeding preparations such that they were often expecting experiments even if we tried to conceal the bags (cf. de Waal 1992). All sharing sessions were videotaped and subsequently coded using Mangold InterAct or the

207 Noldus Observer. In addition to all food interactions we recorded grooming and other affiliative
208 behavior (embrace, socio-sexual behavior) throughout the day using all occurrence sampling, but
209 here we restrict analyses to grooming one hour immediately preceding and following each
210 sharing session (as well as during the sharing session). The reason we chose a 1h time window
211 was that this was typically the interval of uninterrupted resting/grooming time between feedings
212 in both zoos; in any longer time period additional interactions would have interfered and diluted
213 the effects (or lack thereof) of one service on another. The bonobos in both PLD groups could
214 not be observed before the morning sharing sessions and also did not have unrestricted access to
215 each other for grooming as individuals were separated into smaller groups for the night. Hence
216 no prior grooming information on these sharing sessions could be included.
217
218 Following Feistner and McGrew (1989), food sharing was defined as the un-resisted
219 transfer of food from one individual (owner) to another (approacher) out of the owner's hand,
220 foot, or mouth. Acquisition of food that was not in physical contact with another individual, such
221 as 'collect near' (de Waal, 1989) or 'recovery' (Boesch & Boesch-Achermann, 1989), was not
222 considered a transfer because individuals never protested such transfers and therefore did not
223 seem to claim ownership. Likewise, forced transfers were not considered as they do not
224 constitute a service that is likely to be reciprocated (Jaeggi et al., 2010a). The majority of un-
225 resisted transfers occurred in the form of passive transfers or tolerated taking; active forms of
226 transfer only occurred among the chimpanzees (Jaeggi et al., 2010a,b). In addition to the
227 occurrence of transfers we also noted the behavior of the approacher, in particular whether they
228 used any socio-positive behavior such as affiliative contact, grooming or socio-sexual behavior

229 and the reaction of the owner as positive (conducive to food transfer), neutral no reaction) or
230 negative (impeding food transfer, see below).
231
232 *Statistical analyses*
233
234 We used generalized linear mixed effects models (GLMM; Bolker et al. 2009) with
235 binomial error distribution to test for the effects of one service on another with the unit of
236 analysis being each owner-approacher dyad that interacted over food for each sharing session.
237 Models with FGS as the dependent variable were weighted by the total number of approaches.
238 We controlled for repeated sampling of the same individuals by including the ID's of owner and
239 approacher as random factors. Furthermore, we included group and species ID (here also
240 equivalent to location) as random factors in the models combining all study groups and group ID
241 in models combining the two bonobo groups. GLMM's were fitted using the lme4 package
242 version 0.999375-42 (Bates et al., 2011) in R 2.14.1 (R Development Core Team, 2012).
243 Statistical significance was assessed at the α=0.05 level. We fitted two different models for each
244 analysis, a '*tit-for-tat model*' and a '*best-fit model*'. The tit-for-tat model included only the
245 previously received service (grooming, food sharing) as a predictor. The best-fit model also
246 included a range of possible control variables (see Hypotheses). We report only the variables
247 retained in the model with the lowest AIC resulting from a stepwise selection procedure. In
248 contrast to previous studies (e.g. de Waal 1997) this allowed us to test for several competing
249 hypotheses at the same time.
250
251 Our response variables to test for short-term contingency and its behavioral mediation were:

- *Food-getting success (FGS)*: Proportion, defined following de Waal (1997) as the proportion of approaches to within arm's reach of a food owner that led to food sharing. We used this as the main sharing measure (rather than number of transfers or amount of food shared) as it controls for differences in the opportunity to share. This model was weighted by the total number of approaches as FGS calculated from a small number of approaches can easily reach very high or very low values.
- *Grooming received after sharing*: Binary, did the former approacher groom the former food owner within 1h after a sharing session?
- *Negative* or *aggressive reaction*: Binary, we scored a *negative reaction* if the owner showed any behavior impeding transfer such as turning away, holding food away, leaving, or aggressing the approacher by threatening, bluffing, or physically attacking. This was also scored as an *aggressive reaction.*

The main predictors for the tit-for-tat models were:

- *Grooming received before sharing*: Binary, did the approacher groom the food owner within 1h before a sharing session? This was the main predictor for models on FGS. We used a binary rather than continuous measure since de Waal (1997) found that the effect of grooming on food sharing was independent of duration.
- *Food-getting success given*: Proportion, what was the FGS the food owner allowed a specific approacher during the previous sharing session? This was the main predictor for models on grooming received after sharing.

The full list of control variables was:

- *Grooming received from third parties before sharing*: binary, did the current food owner receive grooming from individuals other than the current approacher within 1h

before the sharing session? This tests for partner specificity or the 'good mood hypothesis' which would predict indiscriminate sharing after being groomed (de Waal, 1997).

- *Grooming given by food owner before sharing*: binary, did the current food owner groom the current approacher within 1h before the sharing session? This controls for an effect of (the current state of) the relationship as an effect on subsequent sharing by itself would indicate the direction in which services usually flow within the dyad whereas an effect in interaction with grooming received would indicate a fluctuation in the propensity to provide services within the dyad that is consistent with attitudinal reciprocity or shifting market forces in the partner choice model.
- *Relationship quality*: Continuous, calculated following Fraser et al. (2008) as the first factor of a principal components analysis including time spent in proximity, time spent grooming, and proportion of agonistic interactions in which coalitionary support was provided for each dyad (Jaeggi et al., 2010a). This controls for long-term contingency consistent with symmetry-based reciprocity and partner choice.
- *Maternal kinship*: Binary, are the owner and approacher maternal relatives? This controls for kinship biases.
- *Cardinal rank difference*: Continuous, the difference between the cardinal ranks of approacher and owner, calculated as normalized David's scores (de Vries, Stevens, & Vervaecke, 2006). This controls for transfers being due to differences in resource-holding potential as well as for similarity biases proposed for symmetry-based reciprocity

- *Sex combination*: Factorial, female-female (baseline), female-male, male-female and male-male. This controls for biases due to less tangible sex-specific exchanges such as long-term exchange of food for mating (Gomes & Boesch, 2009).

Finally, we allowed for interaction effects between the main predictor variable (grooming or FGS received) and relationship quality, in order to test the social distance hypothesis, as well as with grooming given by owner (for models predicting FGS) in order to further tease apart the effects of contingent exchange and the current state of the relationship. We report each analysis for all groups combined and for the two species separately (with the two bonobo groups combined). We also ran all analyses for the two bonobo groups separately but do not report these results here as the sample sizes were too small to make confident inferences about further differences between them. We used Chi square tests to compare general patterns on the occurrence of grooming and affiliative behaviors around sharing sessions as well as negative or aggressive reactions to food requests.

Results

General patterns

In total, we recorded 1612 approaches to food owners in 836 different dyads of which 239 (14.8%) led to food transfer. Among the bonobos 95 (9.1%) of 1043 approaches in 477 dyads resulted in transfer, significantly less than among chimpanzees (144 of 569, 25.3%, 358 dyads; Chi square test $X^2_1 = 76.5$, $P < 0.001$, cf. Figure 1). The majority of transfers among the

bonobos were from subordinates to dominants (64, 67.3% vs. 31, 32.7%) whereas more were from dominants to subordinates among the chimpanzees (109, 75.7% vs. 35, 24.3%). Finally, among bonobos most transfers were from females to males (61, 64.2%) followed by transfers from males to females (18, 18.9%) and among females (16, 16.8%). No transfers among males were observed. Among chimpanzees, the majority of transfers were from males to female (75, 52.1%), followed by transfers among females (45, 31.3%), from females to males (13, 9%) and among males (11, 7,6%).

Grooming occurred in 64 (13.0%) of 592 dyads that could be observed before a sharing session and subsequently interacted over food. This percentage did not vary significantly across the two species (Bonobos: 14.5%, Chimpanzees: 12.1%, $X^2_1 = 0.41$, $P = 0.52$). On the other hand, grooming occurred in 147 (19.1%) of the 769 dyads that had previously interacted over food and could be observed after a sharing session. This percentage was significantly different across groups, being much lower in the chimpanzee group (Bonobos: 26.9%, Chimpanzees: 7.2%, $X^2_1 = 45.5$, $P < 0.001$, cf. Figure 2).

Short-term contingency

The tit-for-tat models showed a significant effect of grooming on food sharing and vice versa in both species combined (Table 3, tit-for-tat models). However, this effect disappeared when including control variables (Table 3, best-fit models). Indeed, the effect of grooming on FGS became negative, especially for dyads with a low relationship quality as indicated by the

interaction term. The same was true for grooming received from third parties. Sharing was also lower the more the approacher outranked the owner but higher among maternal kin. Grooming received after sharing was entirely explained by the long-term relationship quality of the dyad and not FGS given in the previous sharing session. Thus, the short-term contingency hypothesis was not supported in both species combined as FGS and grooming seemed better explained by general characteristics of the dyad.

(insert Table 3 about here)

Among the bonobos, the tit-for-tat model showed a positive effect of grooming received on FGS which became significant in the best-fit model when controlling for grooming given (Table 4). FGS significantly predicted grooming received after sharing in the tit-for-tat model and remained a strong predictor with a statistical trend in the best-fit model with a smaller but significant effect of relationship quality. Thus, short-term contingency in bonobos seemed consistent with the exchange of one service on another as grooming received predicted food sharing, especially if no grooming was given, and food sharing and relationship quality explained subsequent grooming received.

(insert Table 4 about here)

(insert Figure 1 about here)

Among the chimpanzees on the other hand, the tit-for-tat models showed no significant effect and the main predictors turned negative or disappeared altogether in the best-fit model

366 (Table 4). FGS was negatively predicted by grooming received, both by approachers and third
367 parties, but positively by grooming given and received in dyads with high relationship quality, as
368 indicated by the interaction terms. This suggests an effect of the current state of the relationship.
369 Furthermore, FGS was negatively predicted by relationship quality (except in interaction with
370 grooming) and cardinal rank difference, but positively predicted by kinship. Grooming after
371 sharing was entirely predicted by relationship quality and rank difference. Thus, the probability
372 of providing a service in chimpanzees was best explained by the current state of the relationship
373 and long-term characteristics of the dyad but not by the contingent exchange of one service on
374 another.
375
376 (insert Figure 2 about here)
377
378 Behavioral mediation
379
380 Negative reactions to food requests were observed in 130 (37.5%) of 776 dyads that
381 interacted over food. This percentage was not significantly different in the two species (Bonobos:
382 37.4%, Chimpanzees: 37.7%, $X^2_1 = 0.01$, P = 0.92). Aggressive reactions, a subset of negative
383 reactions, occurred in 35 (4.3%) of 820 dyads which was higher in the bonobos with a statistical
384 trend (Bonobos: 5.2%, Chimpanzees: 2.9%, $X^2_1 = 2.73$, P = 0.099).
385
386 There was no evidence that short-term contingency of grooming on food sharing was
387 mediated by a decrease in negative or aggressive reactions to food requests as the main predictor
388 variables were not significant in the tit-for-tat models and not retained in the best-fit models in

all groups combined or both species separately (Supplementary Table 1). The probability of encountering negative or aggressive reactions seemed better explained by general characteristics of the dyad such as kinship, rank difference, or sex combination than by recent interactions.

Among bonobos, grooming during a sharing session occurred in 32 (6.7%) of 477 dyads that interacted over food and in 24 (5% of dyads) it occurred during approaches to food owners. Affiliative behaviors including grooming occurred in 92 (19.2%) dyads and in 44 (9.2%) they occurred during food approaches. On the other hand, grooming during the sharing session between individuals who interacted over food was never observed among the chimpanzees and affiliative behaviors occurred only in two (0.6%) of 358 dyads who interacted over food, both times during a food approach. Thus, grooming and affiliative behaviors were significantly more frequent in bonobos both during food approaches and during the session generally (Grooming during approaches: $X^2_1 = 18.6$, $P < 0.001$, grooming during session: $X^2_1 = 25.0$, $P < 0.001$, affiliative behavior during approach: $X^2_1 = 29.5$, $P < 0.001$, affiliative behavior during session: $X^2_1 = 71.8$, $P < 0.001$). This indicates a higher need to reduce tension in a situation involving monopolizable food among bonobos which could have mediated the short-term contingency reported above.

(insert Figure 3 about here)

Discussion

411 We tested for short-term contingencies of grooming on food sharing and vice versa in our
412 two closest living relatives, bonobos and chimpanzees, in order to help resolve some of the
413 debate about proximate mechanisms of reciprocal altruism and thus the role of reciprocity in
414 explaining primate and human cooperation more generally. We found significant effects of
415 grooming on food sharing and vice versa, but when controlling for other variables sharing and
416 grooming were better explained by long-term characteristics of the dyad such as kinship,
417 differences in cardinal rank, or services exchanged over longer time periods as measured by
418 relationship quality. There was also no evidence that recent events decreased the likelihood of
419 encountering negative or aggressive reactions to food requests, which has been proposed to
420 mediate contingent exchange (de Waal, 1997). This pattern was true overall and among the
421 chimpanzees, and together with previous findings of long-term contingency of food, grooming
422 and support among the same chimpanzees (Jaeggi et al., 2010a) is consistent with the partner
423 choice model in which the likelihood of providing a service depends on the history of past
424 interactions, outweighing single recent events (Schino & Aureli, 2009; 2010). In addition, the
425 positive interactions between recent grooming and relationship quality found among the
426 chimpanzees (Table 4) do indicate an effect of the current state of the relationship, perhaps
427 consistent with the idea of attitudinal reciprocity (Brosnan & de Waal, 2002; de Waal, 2000) or
428 fluctuations in partner choice due to shifting market forces (Schino & Aureli, 2009; 2010). A
429 system of calculated reciprocity working on top of other forms of reciprocity in cognitively
430 advanced species (Brosnan & de Waal, 2002; de Waal, 1997) was however not supported among
431 the chimpanzees.
432

433 Among bonobos we did find significant effects of grooming on food sharing and vice
434 versa, even after controlling for other factors. But does this really reflect contingent reciprocity
435 in the sense that is of interest to the broader debate on the evolution of cooperation in humans
436 (House et al., in review) and animals (Clutton-Brock, 2009; Hammerstein, 2003)? Bonobos in
437 this study showed little evidence for long-term contingency of food, grooming and support
438 (Jaeggi et al., 2010; de Groot, 2011), why then the observed short-term contingencies? To
439 answer this question we have to describe the food sharing psychology of bonobos compared to
440 chimpanzees. In the wild, chimpanzees after a hunt tend to quickly establish ownership of the
441 carcass followed by the formation of begging clusters in which ownership is rarely contested and
442 food pieces are obtained mainly through tolerated passive transfers in response to more or less
443 persistent begging (e.g. Boesch & Boesch-Achermann, 1989; Gilby, 2006; Nishida et al., 1992),
444 a pattern which is easily replicated in captivity and therefore seems well engrained in the species
445 psychology (Jaeggi et al., 2010a; de Waal, 1989, 1997). A typical such interaction is illustrated
446 in Figure 3 (see also Supplementary Video 1). Unfortunately, relatively little is still known about
447 sharing in wild bonobos but it seems like sharing interactions tend to include few individuals and
448 rates of transfers are relatively low (Fruth & Hohmann, 2002; Hohmann & Fruth, 1993; White,
449 1994) unless they include provisioned food (Kuroda, 1984). In captivity, bonobos are more
450 stressed than chimpanzees by situations involving monopolizable food (Wobber et al., 2010a),
451 and while they tend to monopolize less than chimpanzees of comparable ages (Hare et al., 2007;
452 Wobber et al., 2010b) they fail to use persistent begging as a means to obtain food once
453 ownership has been established, trying instead to snatch food or claim it by force such that
454 success rates are low and the majority of transfers as defined here are forced and directed up the
455 hierarchy (Jaeggi et al., 2010a; de Waal, 1992; cf. General Patterns, Supplementary Video). In

456 fact, it has been noted that “feeding sessions seemed to be of a more tolerant character in the
457 chimpanzee, which appeared inhibited in the use of force” (de Waal, 1992, p.48). Further
458 expressions of tension surrounding monopolizable food may be the significantly lower success
459 rates and higher levels of aggressive reactions to food requests found among the bonobos in this
460 study and indeed the relatively high levels of aggression and oftentimes strong dominance
461 hierarchies formed in zoo-housed bonobos generally (Jaeggi et al., 2010a; Stevens et al., 2005;
462 2008).

463 Thus, our results on short-term contingency among bonobos make sense in light of the
464 considerable tension surrounding monopolizable food. Indeed, bonobos in this study sometimes
465 seemed nervous and reluctant to approach food owners, especially if they were socially distant.
466 Rather than confidently claiming food the way chimpanzees often do, approachers would
467 sometimes hesitantly groom, touch or embrace food owners before attempting to take food
468 (Figure 3). This was hardly ever observed among the chimpanzees. Tension around
469 monopolizable food resulted in significantly higher rates of grooming and other affiliative
470 behaviors during sharing sessions including during approaches to food owners and perhaps
471 grooming in anticipation of and certainly in the aftermath of sharing sessions, which was
472 significantly more common than among chimpanzees. These patterns are consistent with the
473 reported frequent use of grooming and socio-sexual behavior in competitive feeding situations
474 among wild bonobos (Kano, 1980; Kuroda, 1984) and higher levels of grooming compared to
475 chimpanzees during food sharing sessions (de Waal, 1992), which seems to have carried over
476 into the periods immediately preceding and following the sharing sessions. Since grooming is
477 well known to alleviate tension and reduce stress-levels in both groomer and groomee (Dunbar,
478 2010), this might well be the mechanism responsible for the observed short-term contingency. It

479 is nonetheless noteworthy that this mechanism was partner-specific, sensitive to the direction of
480 grooming and not outweighed by long-term characteristics of the relationship (Table 4), which is
481 perhaps consistent with calculated reciprocity (Brosnan & de Waal, 2002; de Waal, 1997).
482 However, this mechanism failed to generate consistent evidence for long-term contingency of
483 food, grooming and support in the same subjects (Jaeggi et al., 2010a; de Groot, 2011) and can
484 therefore not explain the existence of such contingencies in other species (cf. Silk 2002; Schino
485 2007; Schino and Aureli 2009; 2010; Jaeggi and van Schaik 2011).
486
487 *Mechanisms of reciprocity in primates*
488
489 In sum, our results on chimpanzees support a model of primate reciprocity in which
490 services are given based on a tally of past interactions that build up over the course of a
491 relationship, leading to a long-term contingency of services given and received (Schino &
492 Aureli, 2009; 2010; Trivers, 1971). According to this model recent single events are often
493 negligible, explaining the mixed results of studies examining short-term contingencies in
494 primates (Table 1), and exchanges (or statistical measures thereof) become more balanced over
495 time (Frank and Silk, 2009; Gomes et al., 2009; Tiddi et al., 2011). The short-term contingency
496 observed among the bonobos in this study was likely due to a tension-reduction mechanism
497 specific to the food sharing situation, but may nonetheless fulfill the criteria for calculated
498 reciprocity (Brosnan and de Waal, 2002; de Waal, 1997) despite a failure to generate long-term
499 contingency. The same mechanism may well be at work in some of the other positive effects
500 found in the naturalistic studies in Table 1, all of which describe an effect of grooming on
501 another service. Finally, the differences between our tit-for-tat models and best-fit models

emphasize the importance of taking into account the general characteristics of the subjects' relationships as these outweighed any short-term effect among the chimpanzees. Overall, these results suggest that long-term contingencies might be more common in primate groups when the importance of single events is outweighed by a tally of past interactions. However, when mechanisms to reduce tension are needed short-term contingencies may arise.

The most likely psychological mechanism for long-term contingency is for the probability of providing a benefit to a specific other at any given time to be mediated by some kind of 'relationship score' (Jaeggi et al., 2010b; Schino & Aureli, 2010; Tooby & Cosmides, 2008; Tooby et al., 2008). This score should minimally encode a tally of past interactions, but could possibly also be combined with a kinship coefficient, relative formidability, or dominance rank of ego and other (Jaeggi et al., 2010b; Lieberman et al., 2007; Sell et al., 2009; Tooby & Cosmides, 2008; Tooby et al., 2008). However, this does not require keeping a detailed memory of all past interactions, rather, recent events may only be noted if they deviate substantially from the value the score has asymptoted to over the course of the relationship (Tooby & Cosmides, 2008; Tooby et al., 2008). That such fluctuations do occur is evidenced by the interactions between recent grooming and relationship quality found here (Tables 3 and 4). Computationally, this tally is probably encoded as the likelihood of providing a service to another individual given a certain cost-benefit situation, but subjectively it may be experienced as an emotion such as sympathy (Jaeggi et al., 2010b; Tooby & Cosmides, 2008; Tooby et al., 2008).

Cognitive constraints on reciprocity?

525 It has been argued that primates, and possibly even humans are unlikely to have the
526 cognitive requirements for a tit-for-tat like psychology involving a detailed memory of past
527 interactions and effects of one service on another due to limitations in memory, temporal
528 discounting, and other necessary preconditions (Stevens & Hauser, 2004; Stevens et al., 2010;
529 Stevens et al., 2005). However, astonishing dedicated cognitive specializations are found in
530 many organisms, for instance the incredible spatial memory, causal understanding of tools, and
531 understanding of others' intentions in corvids (Emery & Clayton, 2004). These and other
532 examples of surprising cognitive abilities in animals (Shettleworth, 2009) suggest that animals
533 can evolve almost any dedicated cognitive abilities, provided that selection pressures are strong
534 enough. The lack of a tit-for-tat psychology in primates therefore suggests that there was simply
535 no need for them to evolve such abilities. Our study adds some weight to this notion by showing
536 that short-term contingencies were absent in the presence of more loosely regulated long-term
537 contingency in the chimpanzees, and that short-term contingencies were largely restricted to
538 tension-reduction mechanisms such as grooming in a competitive situation in the bonobos and
539 perhaps other naturalistic studies with positive effects (cf. Table 1). Like others (Schino &
540 Aureli, 2009; 2010; Tooby & Cosmides, 2008; Tooby et al., 2008; Trivers, 1971), we therefore
541 suggest that a long-term statistical contingency between services given and received mediated by
542 stable social relationships and the computation of a tally of past interactions is enough to be
543 favored by natural selection on reciprocal altruism. Such a mechanism may also explain most of
544 the contingencies observed in human populations (e.g. Gurven, 2004a) with a sensitivity for
545 short-term contingencies being acquired relatively late in development (House et al., in review)
546 and perhaps only necessary for interactions with relative strangers with little history of past
547 interactions.

548

549 *Future directions*

550

551 In long-lived species with stable groups and individual recognition there is ample
552 opportunity for reciprocal interactions (Trivers, 1971) hence short-term contingency is always
553 likely to be outweighed by the effects of the two partners' longer history of interactions. The
554 only time one should therefore see a strong effect of recent interactions is when dyads are newly
555 formed and start their relationship from scratch (Roberts & Sherratt, 1998). Examples of this in
556 primate would be when individuals immigrate into a new group or start entering the social fabric
557 of adults as they mature. A naturalistic experiment of the same kind is provided in zoos when
558 new individuals are introduced into a social group. Future work into the psychological regulation
559 of reciprocity in primates should therefore focus on such newly formed dyads and test whether
560 recent interactions weigh heavily in the beginning, how many recent interactions are taken into
561 account, and how long it takes for a tally of past interactions to outweigh single events. Finally,
562 the differences between our tit-for-tat and best-fit models draw attention to the fact that the
563 behavior of nonhuman primates under investigation is strongly influenced by the history and
564 general characteristics of their social relationships which should therefore be controlled for in
565 any future study on the proximate regulation of reciprocity or cooperation more generally.

566

Acknowledgements

We are very grateful to the directors and staff of the Abenteuerland Walther Zoo and Dierenpark Planckendael for their great support, to C. Rudolf von Rohr, M. van Dongen, A. Ziltener, and C. Hrubesch for help with data collection, and to C. M. Sober for assistance with data entry. We also thank M. van Noordwijk at the University of Zurich and M. Gurven, J. Tooby, L. Cosmides, and all members of the Evolutionary Anthropology Research Group and the Center for Evolutionary Psychology at UCSB for useful discussions. AJ was supported by grants from the Cogito Foundation (S-106/06), the Swiss National Science Foundation (PBZHP3-133443), the A. H. Schultz Foundation, and a junior fellowship from the Sage Center for the Study of the Mind. The Flemish government provided structural support to the Centre for Research and Conservation. This research complied with all legal requirements for the ethical treatment of animals.

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789 **Figure Legends**

790 **Fig.1:** Does grooming lead to more food sharing? Mean +SD food-getting success if the
791 approacher did (grey bars) or did not groom (white bars) the food owner immediately prior to the
792 sharing session in bonobos and chimpanzees. The effect was significant only among bonobos
793 (Table 4).

794 **Fig.2:** Is more food sharing rewarded by more grooming? Grooming (yes/no) of previous food
795 owners by previous approachers immediately following a food sharing session as a function of
796 previous food-getting success by those approachers. Lines are fitted on the raw data with
797 univariate generalized linear models and shaded areas represent 95% confidence intervals. The
798 effect was significant only among bonobos (Table 4).

799 **Fig.3**: Typical examples of food interactions among bonobos and chimpanzees (see also
800 Supplementary Video): a) a bonobo female (front) established affiliative contact with another
801 female in possession of food (back) before attempting to take food (picture credit J. M. G.
802 Stevens); b) two chimpanzee females (left and right) confidently claim food from a male in
803 possession of food (center) who offers little resistance (picture credit A. V. Jaeggi).

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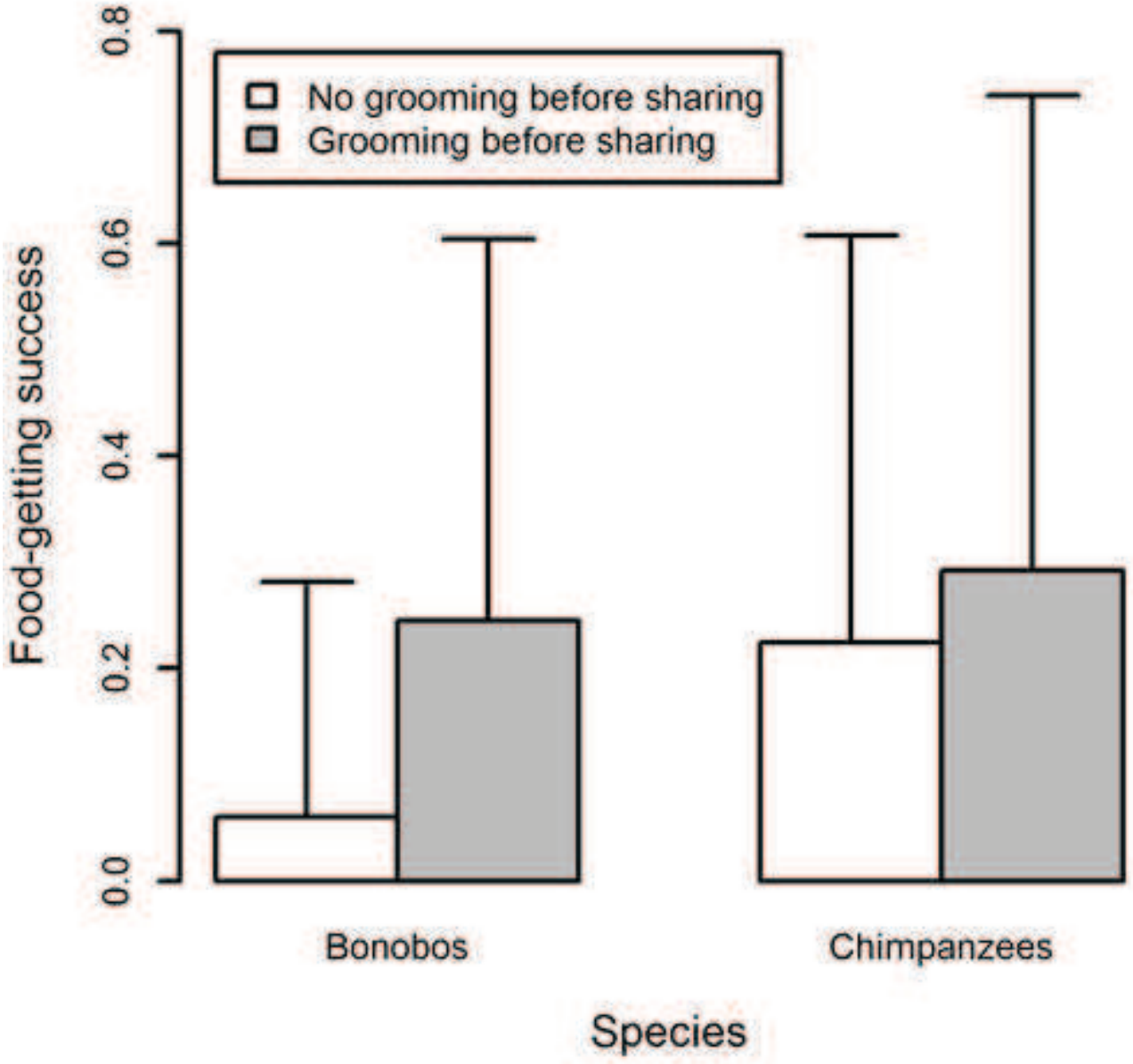

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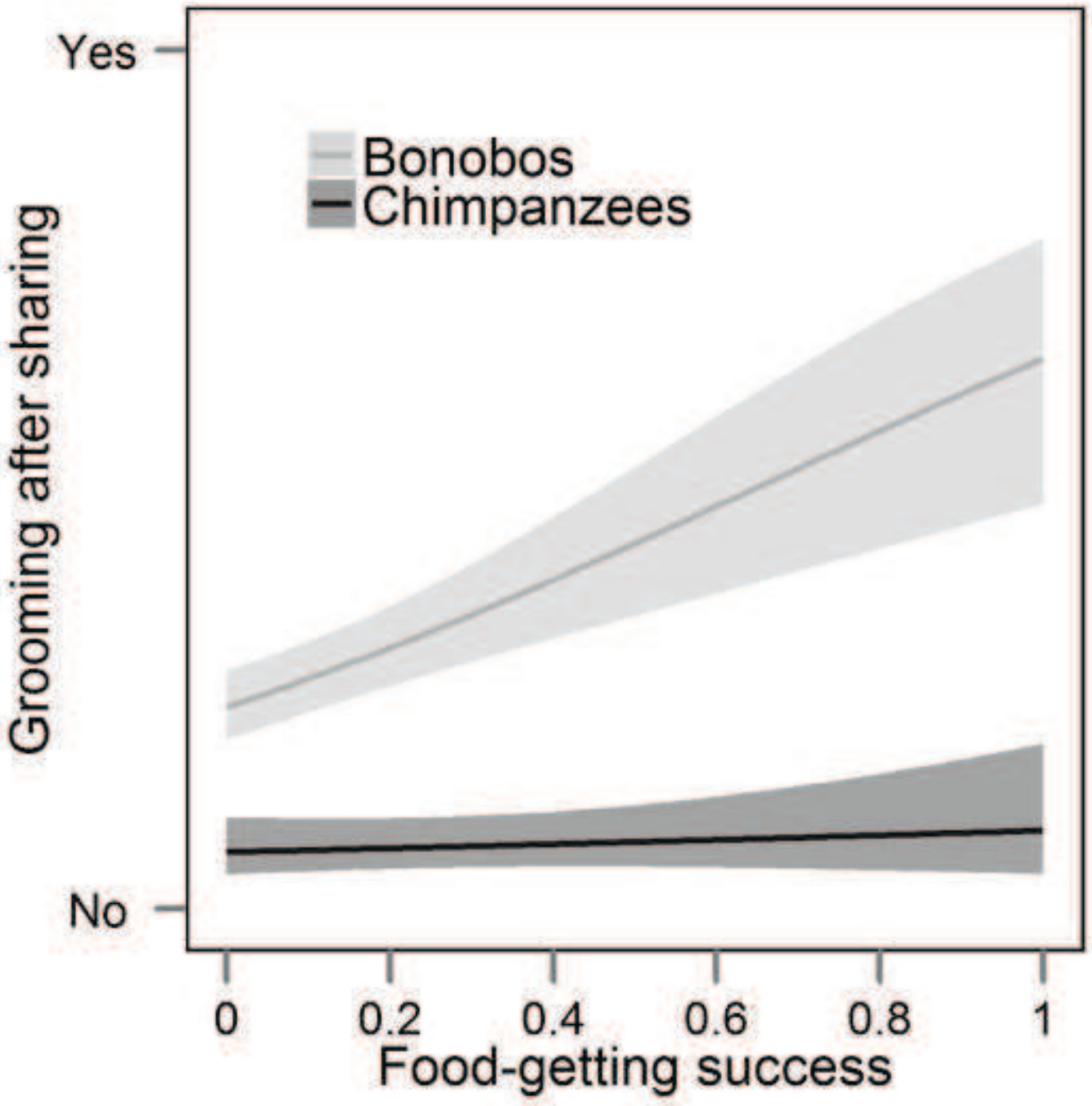

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Table 1: Overview of all experimental studies testing for short-term contingency in non-human primates, divided into those that employed a naturalistic vs. artificial design (see text for details), and those that did or did not find an effect of one service on another (as concluded by the respective authors). There is a significant association between naturalistic design and positive result (Fisher's exact $P<0.05$; different experiments, groups or species in the same study are treated as independent units: Melis et al. 2008, Pele et al. 2009)

Design/Effect	Yes	No
Naturalistic	**7**[a]	**1**[b]
Artificial	**4**[c]	**11**[d]

[a] Seyfarth and Cheney 1984; Hemelrijk 1994; de Waal 1997; Koyama et al. 2006; Cheney et al. 2010; Schino and Pellegrini 2011; Tiddi et al. 2011

[b] Schino et al. 2007

[c] de Waal 2000; de Waal and Berger 2000; Hauser et al. 2003; Dufour et al. 2009

[d] Melis et al., 2008; Brosnan et al. 2009; Brosnan and Beran 2009; Pele et al. 2009; Yamamoto and Tanaka 2009; Yamamoto and Tanaka 2010; Horner et al. 2011

Table 2: Overview over the study groups, study periods, and food sharing data

Group	Species	Location	Demog.	Period	Obs.h	Exp.	FT
GOS	Chimpanzees	Gossau	8 ♀, 3 ♂	Oct 2007–Feb 2008	82	30	144
PLD2008	Bonobos	Planckendael	3 ♀, 3 ♂	Apr–May 2008	125	53	31
PLD2010	Bonobos	Planckendael	3 ♀, 3 ♂	July 2010	100	30	64

Gossau = Abenteuerland Walter Zoo, Gossau SG, Switzerland; Planckendael = Dierenpark Planckendael, Mechelen, Belgium; Demog. = Demographic composition (adults only); Period = Study period; Obs.h = Observation hours; Exp. = Number of experiments; FT = Number of food transfers

Table 3: Results of the GLMM's predicting short-term contingencies of grooming on food sharing and *vice versa* in all study groups combined. GLMM's control for approacher, owner, group and species ID. The tit-for-tat model includes only the predictor for short-term contingency whereas the best-fit model includes those control variables that yield the lowest AIC (see Methods for full list of controls). The sample size is 492 / 769 dyads that interacted over food for which we had data on previous / subsequent grooming

		Tit-for-tat model	***Best-fit model***
		AIC = 505.7	**AIC = 345.3**
Response variable	**Predictors**	**b (±SE)**	**b (±SE)**
Food-getting success	(Intercept)	-2.83 (±0.84)***	-2.77 (±0.98)*
	Grooming received	0.63 (±0.27)*	-1.31 (±0.70)^{t}
	Grooming received by third parties		-0.81 (±0.26)**
	Cardinal rank difference		-0.37 (±0.13)**
	Maternal kinship		1.76 (±0.47)***
	Grooming received * Relationship quality		1.24 (±0.40)**
		AIC = 649.4	**AIC = 613.2**
Response variable	**Predictors**	**b (±SE)**	**b (±SE)**
Grooming received	(Intercept)	-2.16 (±0.52)***	-2.13 (±0.50)***
	Food-getting success	0.89 (±0.32)**	

Relationship quality	0.50 (±0.11)***

[t] P<0.1, * P<0.05, ** P<0.01, *** P<0.001

Table 4: Results of the GLMM's predicting short-term contingencies of grooming on food sharing and *vice versa* in the two species seperately. GLMM's control for approacher, owner, and group ID (only bonobos). The tit-for-tat model includes only the predictor for short-term contingency whereas the best-fit model includes those control variables that yield the lowest AIC (see Methods for full list of controls). The sample size is 186 / 463 dyads that interacted over food for which we had data on previous / subsequent grooming for the bonobos and 306 dyads for the chimpanzees

		BONOBOS		**CHIMPANZEES**	
		Tit-for-tat model	***Best-fit model***	***Tit-for-tat model***	***Best-fit model***
		AIC = 109.3	**AIC = 91.6**	**AIC = 384.6**	**AIC = 238.3**
Response variable	**Predictors**	**b (±SE)**	**b (±SE)**	**b (±SE)**	**b (±SE)**
Food-getting success	*Intercept*	-5.42 (±1.23)***	-4.78 (±0.82)***	-1.33 (±0.25)***	-1.39 (±0.28)***
	Grooming received	0.54 (±0.47)	1.14 (±0.39)***	0.40 (±0.33)	-2.76 (±1.78)
	Grooming received by third parties				-0.72 (±0.29)*
	Grooming given		-0.89 (±0.59)		
	Relationship quality				-0.31 (±0.18)^{t}
	Cardinal rank difference				-0.41 (±0.18)*
	Maternal kinship				1.44 (±0.78)^{t}
	*Grooming received * Relationship quality*				3.57 (±1.85)^{t}
	*Grooming given * Relationship quality*				0.47 (±0.31)

Response variable	Predictors	AIC = 482 b (±SE)	AIC = 465.7 b (±SE)	AIC = 164.8 b (±SE)	AIC = 144 b (±SE)
Grooming received	*Intercept*	-1.51 (±0.34)***	-1.54 (±0.28)***	-2.67 (±0.32)***	-2.59 (±0.27)***
	Food-getting success	1.27 (±0.44)**	0.86 (±0.45)^{t}	0.37 (±0.54)	
	Relationship quality		0.56 (±0.14)***		0.16 (±0.23)
	Cardinal rank difference				0.42 (±0.24)^{t}

28 ^{t} P<0.1, * P<0.05, ** P<0.01, *** P<0.001

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